Unraveling the relative importance of factors driving post-fire regeneration trajectories in non-serotinous *Pinus nigra* forests

Running head: Drivers of post-fire regeneration trajectories in non-serotinous pinewoods

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Abstract

In the Mediterranean, non-serotinous pinewoods are suffering an increasing occurrence of high-severity crown fires that usually drive vegetation shifts to fire-adapted communities and a decrease in pine-dominated area. Here we used a case-study approach on a large area dominated by *Pinus nigra* Arn. ssp. *salzmannii* burned in 1998 to gain further understanding of the relative importance of different factors related to local topography (elevation, aspect, slope, curvature), pre-fire vegetation (land-use history, canopy cover) and fire behavior (burn severity, presence of unburned patches) as drivers of post-fire regeneration dynamics. The results find that pine shows locally resilient responses driven mainly by factors related to fire effects (presence of unburned patches) and the characteristics of the pre-fire vegetation (i.e. stable forest areas). When fire-induced changes from pine dominance to other types of vegetation occurred, landscape 15 years post-fire was dominated by woody vegetation, with some rare grassland communities emerging under very specific conditions (mountain ridges, hilltops and rocky sites). Conversion from forest to shrubland occurred mainly in the most xeric sites (south-facing areas, in some cases with steep slopes) and areas dominated by young pine stands prior to the fire. We found manageable factors such as the pre-fire structure and composition of the vegetation strongly determine the occurrence of post-fire regeneration trajectories dominated by tree species regeneration. This knowledge can be used to define preventive management strategies oriented to direct regeneration dynamics in anticipation of fire occurrence. At landscape level, managing forest fuels to favor the occurrence of unburned patches and modify their spatial distribution along the burned landscape will favor a more resilient pine response. At stand level, adjusting silvicultural interventions to favor the natural establishment of late-successional tree species will favor post-fire oak regeneration.

Additional keywords: *Mediterranean pinewoods*, *Quercus*, crown fires, resilience, vegetation shift, unburned patches, pre-fire vegetation.

1. Introduction

Fire is an important ecological factor in pine-dominated forest ecosystems, but not all pine species share the same fire regime and the same type of responses to this disturbance (Agee, 1998; Keeley and Zedler, 1998; Pausas, 2015). Some pine species, defined as fire-tolerators, present a number of traits (i.e. thick basal bark, self-pruning) that allow them to survive under frequent understory fires (Keeley, 2012; Pausas, 2015). These species, in contrast, are usually sensitive to crown fires because they lack direct post-fire regeneration mechanisms (i.e. they are unable to resprout or to produce serotinous cones or seeds able to resist the high temperatures reached during this type of fires). These characteristics usually cause these pinewoods to shift toward different post-fire vegetation states (Rodrigo et al., 2004; Keane et al., 2008). In the Mediterranean, forests dominated by non-serotinous fire-tolerators such as Spanish black pine (*Pinus nigra* Arn. ssp. *salzmannii*) or Scots pine (*P. sylvestris* L.) have suffered an increase in the number of catastrophic crown fires during the last decades (Pausas et al., 2008; Retana et al., 2012; Vilà-Cabrera et al., 2012). This has been attributed to a combination of factors related to changes in land-use (i.e. abandonment of traditional rural practices) and climate warming (Pausas, 2004; Loepfe et al., 2010). The increased drought and hot spells predicted for the coming decades and the associated increase in fire risk are considered to put at high risk the future persistence of certain populations of such pine species (particularly those located in the southern distributional edge) (Vilà-Cabrera et al., 2012).

The nature of vegetation changes in forests dominated by non-serotinous pines affected by crown fires (and particularly whether they move toward early-successional communities such as grasslands or shrublands or toward new forest types dominated by other tree species) will depend on a complex array of factors. These factors include the characteristics of the fire event, the environmental conditions of the affected area and the pre-fire forest attributes. Fire behavior, especially fire severity and disturbance legacies (i.e. residual canopy cover, type of post-fire seedbed, distance from the surviving seed trees, etc) are known to strongly influence both the type and success of post-fire vegetation recovery in a given burnt area (e.g. Broncano et al., 2005; Bonnet et al., 2005; Lentile et al., 2007; Vacchiano et al., 2014). Climate and topography have also been shown to significantly modulate regeneration patterns at landscape level, mostly because they drive soil moisture distribution (e.g. Keeley and Keeley, 1981; Pausas et al., 2004; Buhk et al., 2006; Coop et al., 2010). Post-fire recovery after high-intensity crown fires is also largely dependent on the availability of seeds and vegetative propagules (stems, roots, etc) in the burned stands. In the case of pinewoods non-adapted to crown fires, for example, the presence of resprouting tree species (e.g. *Quercus* ssp.) can prove essential for rapid post-fire forest recovery (Baeza et al., 2007; Puerta-Piñero et al., 2012).

The role of each of the abovementioned factors in driving post-fire regeneration trajectories has been investigated in a number of studies, but there are still very few large-scale integrative works assessing the relative importance of each of these individual factors. While some of these factors (e.g. local topography, climate or land-use history) cannot be modified by silvicultural interventions, others (e.g. fire effects and pre-fire vegetation attributes) can be at least partially managed by means of preventive silvicultural practices. Consequently, further insight into the relative importance of the manageable factors would better inform the suitability of preventive management strategies to prevent undesired vegetation shifts. Here we address this issue using a large wildfire recorded in 1998 that burned a forest area dominated by European black pine in the central region of Catalonia (NE Spain). For this purpose, we used a previous assessment of post-fire regeneration types in the area affected by this wildfire and we generated models for predicting the occurrence of each regeneration type from a set of topographic, fire behavior, and pre-fire forest cover attributes. The aim was to answer the following questions: (*i*) what is the relative importance of factors related to topography, fire behavior, and pre-fire forest cover in enabling autosuccession in forests dominated by pine species non-adapted to crown fires?; (*ii*) which of these factors are the most important drivers of fire-induced change towards different alternative vegetation states? We hypothesized that apart from the presumably strong influence of topography, factors related to fire behavior such as burn severity or the abundance of unburned patches will largely drive direct pine regeneration, while the attributes of the pre-fire forest cover will chiefly shape the occurrence and success of regeneration of resprouting tree species ahead of shrublands or grassland communities.

2. Materials and Methods

2. 1. Study area

The study was conducted in an area in the central region of Catalonia (NE Spain) affected by a large forest fire (Fig. 1) in 1998 that burned nearly 24,000 ha, leading to almost complete loss of forest cover (Rodrigo et al., 2004). Inside the total burned forest area, our study focused on a roughly 2000-ha portion located in its southeastern part (between 1° 33' 48'' and 1° 38' 39'' E, and 41° 45' 4'' and 41° 50' 2'' N, DATUM WSG84) (Fig. 1). Prior to the fire, the vegetation in the area was composed of the typical Mediterranean mosaic-like landscape, consisting of cultivated land and scrubland interspersed with forest areas, these last being mainly dominated by pine and/or oak species. The forest area was dominated by Spanish black pine (*P. nigra*) prior to the fire. Black pine forests were either pure stands or two-layered stands with pine dominating the overstory and resprouting hardwoods (mostly oaks) appearing frequently in the understory (Burriel et al., 2004). The area presents gentle relief with low hills mostly oriented W-E ranging in elevation from 480–910 m above sea level (a.s.l.), and formed by folded structures of sedimentary carbonate rock (mainly lutite, marlstone and limestone) and gypsum sediments. Climate in the area is dry-sub-humid to sub-humid Mediterranean climate according to the Thornthwaite index, characterized by a mean annual precipitation of around 650 mm and a mean annual temperature of around 12ºC (Ninyerola et al., 2005). Rainfall is usually concentrated in autumn and spring. In summer, short convective storms also provide significant precipitation input (around 150 mm in average during the summer), but the occurrence of summer dry periods is not unusual.

A total of 1,915 ha of Spanish black pine (*P. nigra*) forests that totally burned (i. e. with no vegetation remaining after the fire) in 1998 were selected for the assessment of the factors driving post-fire regeneration trajectories (Fig. 1). Areas affected by roads, agricultural fields and other non-forest uses had previously been excluded from the analysis. Some green islands (i.e. patches of adult trees that survived the fire) were found within the burnt area. When implemented, post-fire management consisted of generalized salvage logging (cut and deadwood removal) that was mostly executed during the first winter after the fire.

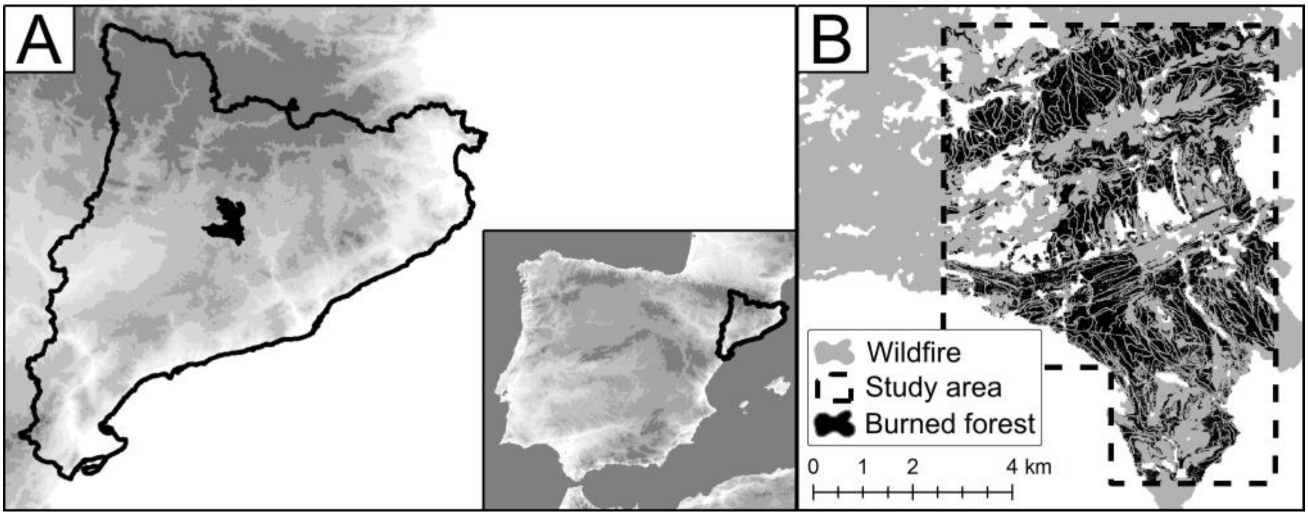

Fig. 1. Location and boundaries of: A) the 1998 wildfire in the Iberian Peninsula and Catalonia region; B) the study perimeter delimiting the burned forest area used in this assessment, for which post-fire regeneration types were developed and mapped by Martín-Alcón et al. (2015a). Areas occupied by roads, agricultural fields and other non-forest uses were excluded from the analysis.

2. 2. Classification and characteristics of post-fire regeneration types

Martín-Alcón et al. (2015a) had previously classified post-fire regeneration in the burned forest area into five post-fire regeneration types. This classification was based on analysis of remote sensing data from airborne LiDAR and multi-spectral imagery calibrated with field data measurements (from 44 field plots). It was based on the vegetation growing naturally in the burned area almost 15 years after the occurrence of the wildfire, at a time when all the species with regeneration potential in the area had likely been established (Gracia et al., 2002). The final classification algorithm classified each 10*x*10 meter portion of the burned area into the following post-fire regeneration types (Table 1): two types matching to areas dominated by soil/herbaceous (T1) or shrub layers (T2) with very low or no tree-species regeneration; a third type showing low-to-moderate tree cover, dominated by hardwood regeneration (T3); and the last two types presenting high cover of tree species—one clearly dominated by hardwood regeneration (T4), the other dominated by pine regeneration (T5)—. The hardwoods dominating tree-species regeneration in types T3 and T4 are marcescent oaks (*Quercus faginea* Lam. and *Q. cerrioides* Willk. & Costa) and the evergreen oak *Q. ilex* L. Other species of the genus *Sorbus*, *Acer*, *Prunus*, etc. are also present but only in a scattered way. The pine species dominating regeneration type T5 is black pine. Finally, the shrub species appearing in all the regeneration types are mainly *Quercus coccifera*, *Crataegus monogyna*, *Viburnum lantana, Rubus ulmifolius* and *Buxus sempervirens* and less frequently (although locally abundantly) *Rosmarinus officinalis*, *Juniperus oxycedrus*, *Prunus spinosa*, *Cornus sanguinea, Genista scorpius* and *Rhamnus alaternus*. According to the post-fire regeneration assessment, regeneration type T4 is the most abundant in the study area, covering 43.6% of the burned area; types T3 and T2 cover 18.9% and 16.3%, respectively; and types T5 and T1 are the least abundant, at 11.5% and 9.7%, respectively (Table 1).

Our initial response variable was a categorical variable that classified each subject (i.e. each one of the 10*x*10 meter plots of burned forest area) into one of the five abovementioned regeneration types. As we suspected our response variable to feature significant spatial autocorrelation, we explored changes in the join-count statistic (Cliff and Ord, 1981) as a function of the Euclidian distance between the plots classified in each one of the regeneration types. As this analysis showed high autocorrelation at low distance classes (up to 30-50 m), regular sub-sampling was applied (Munroe et al., 2004). Thus, one of each of the five points in both the *x*- and *y*-axes (of the 10*x*10-m grid) was sampled, thus yielding a total of 7,702 plots (Table 1). The new subset of plots no longer presented significant autocorrelation according to the join-count statistic. For this subset of plots, a set of explanatory variables was computed.

Table 1. Forest regeneration type with descriptions (from Martin-Alcon et al. 2015), and number of 10*x*10-meter plots corresponding to each type (i) in the entire study area and (ii) in the subsample used for the subsequent analyses.

Regeneration type	Description	Short name	Percentage of occupied area (%)	Total number of plots in class	Number of plots after regular subsampling
T1	Very low woody vegetation cover; absence of tree species regeneration.	Low woody	9.64	18,455	739
T2	Very low tree regeneration but remarkable shrub cover.	Shrubby	18.94	36,263	1,523
T3	Dominance of hardwoods regeneration in low to moderate cover, mixed with shrubs.	Oaks low	16.30	31,204	1,190
T4	Dominance of hardwoods regeneration in high cover.	Oaks high	43.61	83,507	3,371
T5	Dominance of pine regeneration in moderate to high cover.	Pines	11.52	22,059	879

2. 3. Topographic attributes

Among the potential topographic drivers of post-fire regeneration trajectories, we selected four variables derived from remote-sensing data: elevation, aspect, slope and curvature. Elevation was extracted from a 5-m-resolution digital elevation model (DEM), and in the study area is directly related to plot position along the slope gradients. Aspect was pre-transformed using the cosine transformation into a northness index to more adequately reflect the variation between north and south exposures. Northness index increased from -1 on south exposures to 1 on north exposures, with east and west aspects given a value of 0. This is a key gradient under Mediterranean climates, since the higher amount of radiation received in south-facing slopes significantly increases the evaporative demand to which plants are exposed. Finally, slope and curvature of the terrain were extracted from the 5-m-resolution DEM, and both were considered local topography attributes highly related to the soil water content distribution along a given slope (Gómez-Plaza et al., 2001). The terrain curvature was calculated following the equation proposed by Moore et al. (1991) with positive values indicating convex terrain while negative values indicate concave terrain.

2. 4. Estimation of land-use history and pre-fire forest cover

A second set of candidate variables to explain the distribution of post-fire regeneration trajectories was related to the pre-fire vegetation attributes and land-use history. First, we wanted to assess the relative importance of previous land use on post-fire regeneration trajectories (addressed in Puerta-Piñero et al., 2012). For this purpose, we used an object-oriented semi-automatic image analysis on the most ancient aerial photographs in the area (taken in 1956 as grey-scale 1-m-resolution images). The analysis was based on patch-level segmentation and a later classification of land-cover objects according to their spectral signatures and texture attributes. The following land-cover classes were delineated and assigned to each 10*x*10 portion of burned land (Fig. 2): (*i*) 'cultivated land', including agricultural fields and other highly altered areas (roads and paths, farms, etc.); (*ii*) 'non-wooded land', including areas of natural vegetation with no or only scattered trees; (*iii*) 'open woodland', for woodlands presenting low-to-moderate tree cover (i.e., below 30% of tree canopy cover); and (*iv*) 'closed woodland', for woodlands presenting moderate-to-high tree cover (i.e., above 30% of tree canopy cover). In addition, we wanted to assess the relative importance of pre-fire tree canopy cover (TCC), which is known to highly affect the characteristics of the understory vegetation (Coll et al., 2011; Martín-Alcón et al., 2015b). To do this, a new object-oriented semi-automatic image analysis was executed on 50-cm-resolution grey-scale aerial photographs taken three years before the fire (in 1995). The analysis consisted in generating a rule-set based on fine-resolution segmentation and a classification of tree-cover objects according to their spectral signatures and their position with respect to other objects previously identified as tree shades. Both image analyses were performed in eCognition Developer 8.9 software.

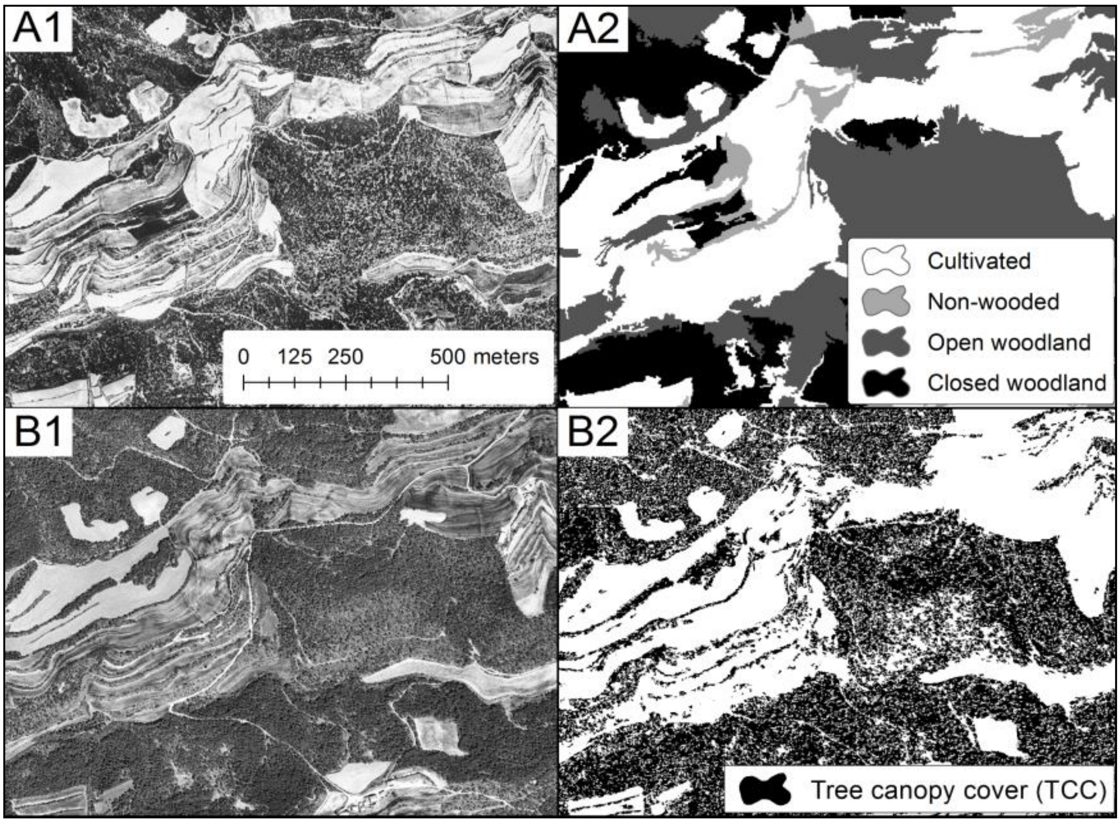

Fig. 2. Example of aerial photographs from 1956 (A1, more than four decades before the wildfire) and 1995 (B1, three years before the wildfire), and the resulting information after object-oriented semi-automatic image analysis for 1956 cover types (A2) and 1995 tree canopy cover (B2).

2. 5. Estimation of burn severity and influence of unburned areas

The last set of explanatory variables was related to the characteristics of the wildfire. First, we computed the Relative Differenced Normalized Burn Ratio (RdNBR) (Miller et al., 2009) as a proxy of burn severity in the study area. The RdNBR is a variant of the Differenced Normalized Burn Ratio (dNBR) (Key and Benson, 2006) that accounts for the relative amount of pre- to post-fire change by dividing dNBR (the absolute amount of pre- to post-fire change) by pre-fire NBR value. The Normalized Burn Ratio (NBR), which is a vegetation index especially suitable for the discrimination of burned areas, was first computed from 30-m-resolution Landsat TM NIR and SWIR bands (4 and 7, respectively). The pre-fire image was taken in 1992, which was the closest available image to the wildfire date, and the post-fire image was taken in 1999 (the year after the fire). Both images were taken during the second half of July. Values of RdNBR in the range 300-600 indicate moderate burn severity, while values higher than 600 indicate high severity (Miller and Thode, 2007). Finally, we computed a variable related to the location of each plot in relation to unburned forest patches. It was calculated as the sum of unburned forest area at a radius of 150 meters from each plot (based on the dispersal range reported by Ordoñez et al. (2006) for *Pinus nigra* ssp. *salzmannii*), and was named as 'Area of unburned patches'.

Table 2. Descriptive statistics of the continuous explanatory variables in the subsample of plots used for the analyses (n = 7,702).

Variable (units)	Mean	Std. Dev.	25th percentile	75th percentile
(a) Topographic variables				
Elevation (m a.s.l.)	724.80	89.08	652.92	798.36
Northness index	0.08	0.72	-0.64	0.83
Slope (°)	18.30	7.22	12.52	23.63
Terrain curvature index	0.10	3.26	-0.84	1.28
(b) Vegetation and land use				
1995 Tree canopy cover (%)	56.64	22.48	45.12	73.36
(c) Fire effect				
RdNBR Index	691.84	173.50	598.16	812.59
Surrounding unburned area (ares)	48.76	73.59	1.00	69.00

2. 6. Statistical analysis

First, we examined Pearson's correlations among the continuous explanatory variables in order to check whether there was any pair of highly-correlated variables potentially affecting the interpretation of the subsequent analyses. The highest significant Pearson's coefficient found was between northness and the TCC in 1995 (Pearson's $r = 0.274$). All the other pairwise correlations gave a Pearson's r below 0.25. We then ran non-parametric Kruskal–Wallis tests in order to check whether there were statistically significant differences between two or more of our regeneration types in terms of our continuous explanatory variables. Kruskal–Wallis tests were used instead of one-way ANOVA because our variables were not normally distributed and variable transformations did not normalize the data. Post-hoc tests were also computed in order to see which pairs of types differed significantly on each one of the explanatory variables. For the only categorical explanatory variable (i.e. land use cover type in 1956), significant differences among groups were analyzed using chi-square tests.

Occurrence probabilities were modeled for each regeneration type and variable importance was computed using the Random Forests method (Breiman 2001). Random Forest (RF) is a nonparametric supervised classification technique that has shown good performance in modeling the occurrence of species or vegetation types (e.g. Evans and Cushman, 2009; Falkowski et al., 2009; Evans et al., 2011). We ran one RF model for each regeneration type. To do this, the response variable for each model was defined as a binary response, i.e. presence (1) / absence (0) of a given regeneration type. The RF technique uses a bootstrap approach to achieve higher accuracies while simultaneously addressing over-fitting problems associated with traditional classification tree models. A large number of classification trees are produced from a random subset of training data (approximately 63% random subset), permutations are introduced at each node, and the most common classification result is selected. In an effort to avoid bias in the prediction caused by imbalanced classes, the number of plots per class in bootstrap samples was always equal to the number of plots of the less frequent class (i.e. n = 739 cases, which is the number of cases in regeneration type T1) (Evans and Cushman, 2009). Bootstrap samples for class 0 ($y = 0$) were always constructed by stratified random sampling with equal proportions among the four regeneration types other than the type of interest (which corresponds to class $y = 1$). We ran each RF model with 10,000 bootstrap replicates (i.e. individual classification trees). Out-of-bag (OOB) error estimates and classification error for the class of interest ($y = 1$; presence of a given regeneration type) were calculated for each tree by classifying the portion of training data not selected in the bootstrap sample, and overall accuracies were calculated by averaging error rates across all trees in the model. No variable selection procedure was applied in any case, because we were more interested in inferring the relative importance of each explanatory variable on the occurrence of a given regeneration type than in developing a parsimonious classification model for each type. A Model Improvement Ratio (MIR) was calculated from standardized importance values for computing variable importance (Evans and Cushman, 2009; Evans et al., 2011). As an output from RF, metrics are ranked in order of importance (*I*) based on the number of times a given metric decreased the mean squared error. However, unlike a raw *I* score, which can be influenced by the total number of metrics in the model, the MIR is comparable among models (Murphy et al., 2010). MIR values were calculated as [I_n/I_{max}], where I_n is the importance of a given metric and I_{max} is the maximum model improvement score. The most important variable in a model always takes the value 1. For the rest of variables, a high positive MIR value (i.e. closer to 1) indicates high importance of the variable, whereas a low-positive or a negative value indicates that the variable is irrelevant.

3. Results

3. 1. Effects of topography on post-fire regeneration trajectories

All the topographic attributes analyzed had effects on the occurrence of the different post-fire regeneration types (Table 3). Elevation and northness were the factors that most strongly differentiated the sites according to type of regeneration they presented (based on chi-square statistics), although slope also had a substantial effect. Post-hoc tests revealed that type T1 (presenting low cover of woody vegetation) occurred at higher altitudes than other types, whereas type T4 (presenting high-density oak regeneration) occurred at significantly lower elevation (Fig. 3). On the other hand, two regeneration types dominated by resprouted oaks (T3 and T4) were found to be more frequent on north-facing slopes, whereas the shrub-dominated type (T2) was more frequent on south-facing slopes. Slope was slightly steeper in the sites that showed shrub or pine dominance (types T2 and T5, respectively) than in the rest of the cases. Finally, the regenerated sites dominated by shrubs (T2) appeared more frequently on convex terrain whereas sites presenting high density of oaks (T4) were found more frequently on concave terrain.

Table 3. Effects of topographic, pre-fire-vegetation, and fire-related variables on post-fire regeneration types (n = 7,702).

Variable	Type	Test	Chi-Square statistic	Significance
(a) Topographic variables				
Elevation	Covariate	Kruskal-Wallis	558.71	<0.0001
Northness index	Covariate	Kruskal-Wallis	327.98	<0.0001
Slope	Covariate	Kruskal-Wallis	192.73	<0.0001
Terrain curvature index	Covariate	Kruskal-Wallis	15.48	0.004
(b) Vegetation and land use				
1956 Cover types	Factor (4-level)	χ^2	262.32	<0.0001
1995 Tree canopy cover	Covariate	Kruskal-Wallis	197.49	<0.0001
(c) Fire effect				
RdNBR index	Covariate	Kruskal-Wallis	177.73	<0.0001
Surrounding unburned area	Covariate	Kruskal-Wallis	143.30	<0.0001

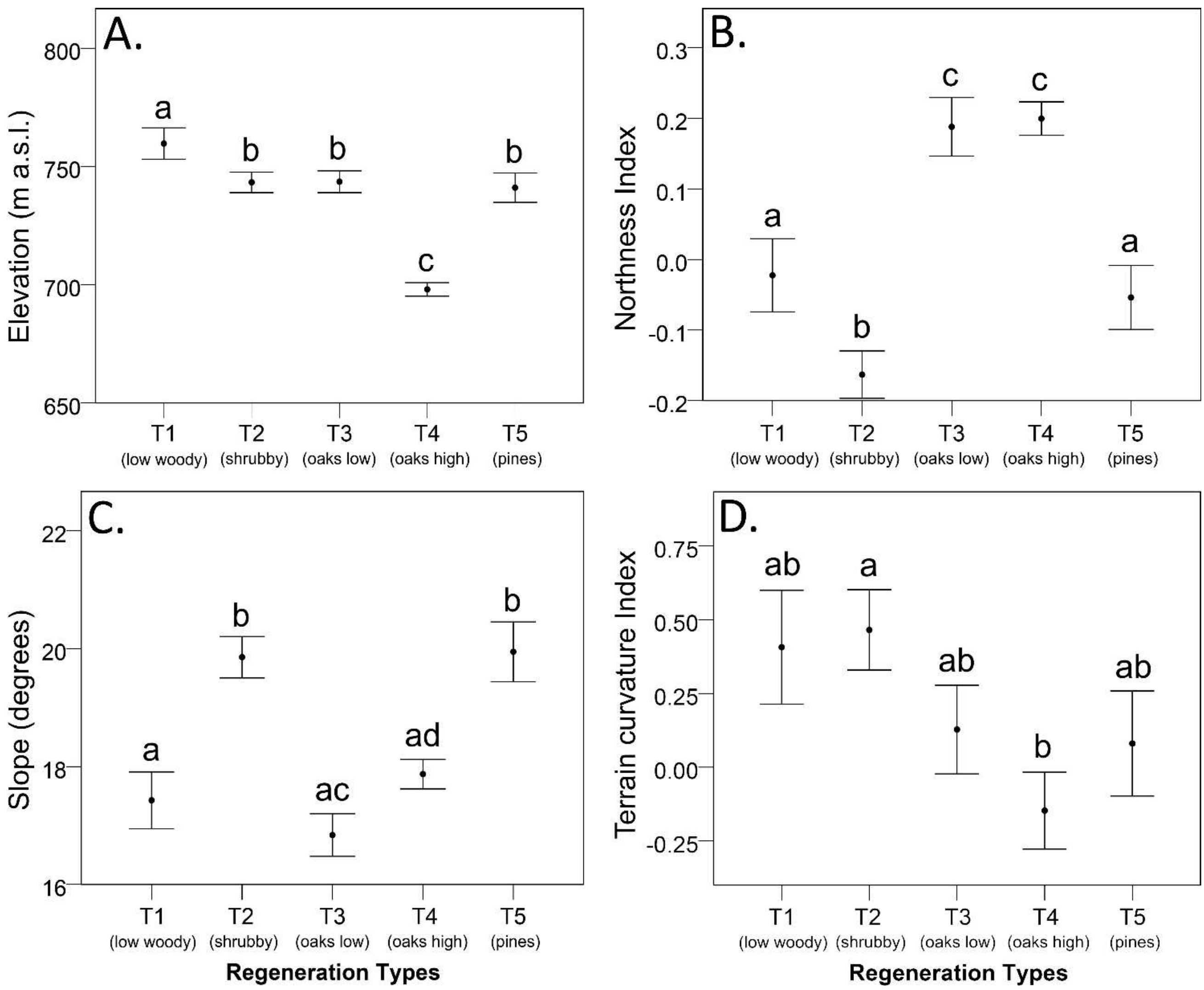

Fig. 3. Mean (± S.E.) values of the four topographic covariates (A, elevation; B, northness index; C, slope; D, terrain curvature) for the plots classified in each of the regeneration types. Different letters indicate significant differences among types according to the Kruskal–Wallis post-hoc tests for all pairwise comparisons.

3. 2. Effects of land-use history and pre-fire forest cover

The land-use type in 1956 and the pre-fire TCC cover showed significant effects on post-fire regeneration (Table 3). The regeneration types with higher abundance of tree-species regeneration (T3, T4 and T5), and especially T4, occurred more frequently at sites with a longer history of dense tree cover (i.e. sites that had been dense woodlands from at least 1956) compared to sites characterized by very low or no tree-species regeneration (T1 and T2) (Fig. 4A). On pre-fire TCC, regeneration types without tree-species regeneration (T1 and T2) were found to occur in sites with significantly lower TCC values than sites with oak and pine regeneration. Between the two oak-dominated regeneration types, pre-fire TCC was slightly higher for T4 than for T3 (Fig. 4B).

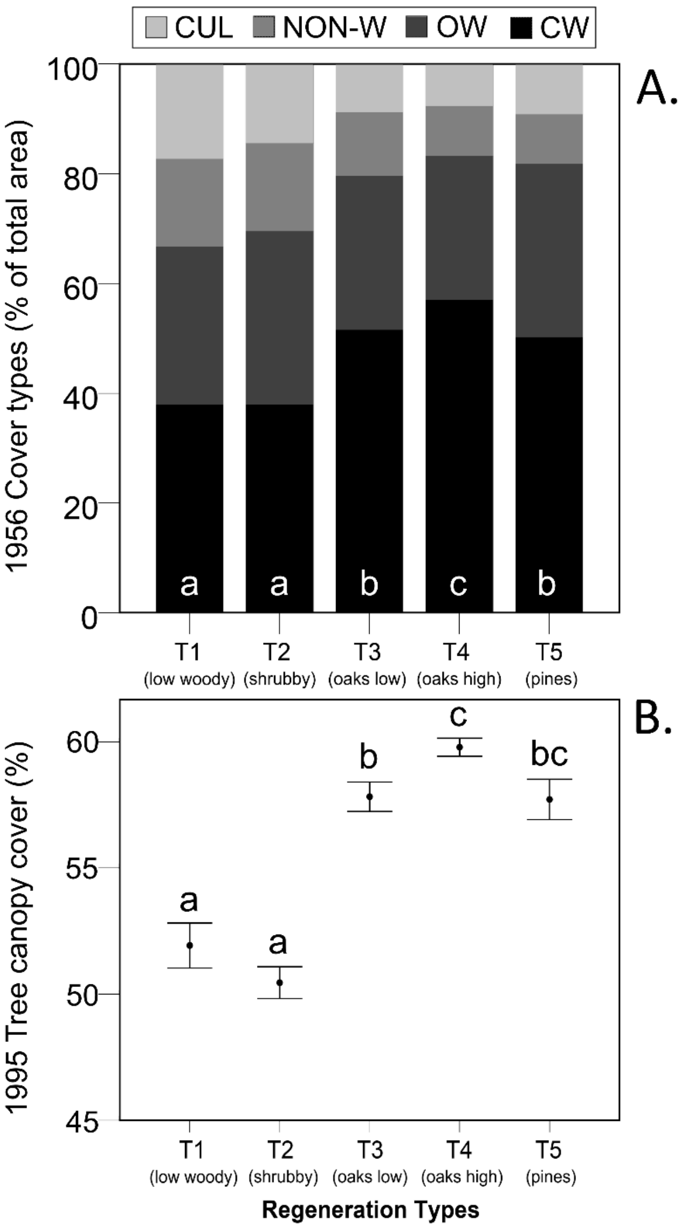

Fig. 4. Differences among regeneration types for the pre-fire-vegetation attributes. (A) Frequency of each 1956 land-use-cover class for the plots classified in each of the regeneration types. Acronymed descriptions of land-use-cover classes (see text for extended descriptions) are: CUL, cultivated land; NON-W, non-woody vegetation; OW, open woodland; and DW, dense woodland. Different letters indicate significant differences among types according to the chi-square tests for all pairwise comparisons. (B) Mean (± S.E.) values of 1995 TCC for the plots in each of the regeneration types. Different letters indicate significant differences among types according to the Kruskal–Wallis post-hoc tests for all pairwise comparisons.

3. 3. Effects of fire behavior

The two factors related to the characteristics of the wildfire (burn severity and presence of unburned patches close to the regenerating areas) played an important role in the occurrence of the different post-fire regeneration types (Table 3). The effect estimate (chi-square statistic) associated to burn severity (as RdNBR) was slightly higher than the effect estimate related to abundance of unburned forest patches around each plot. The resulting RdNBR values (ranging around 500–900) confirmed that the study area was burned at moderate-high to high severity as based on the criteria established by Miller and Thode (2007). Post-hoc tests revealed that fire effects mostly affected the occurrence of pine regeneration (T5) (Fig. 5). On one hand, pine regeneration tended to occur much more frequently in areas in which unburned forest patches were more abundant (Fig. 5B). On the other hand, burn severity was significantly lower in sites marked by pine regeneration than in sites presenting any other regeneration types. Between the two regeneration types dominated by oaks, burn severity was higher for T3 than for T4, and in both cases was significantly higher than in the areas currently dominated by shrubs (T2; Fig. 5A).

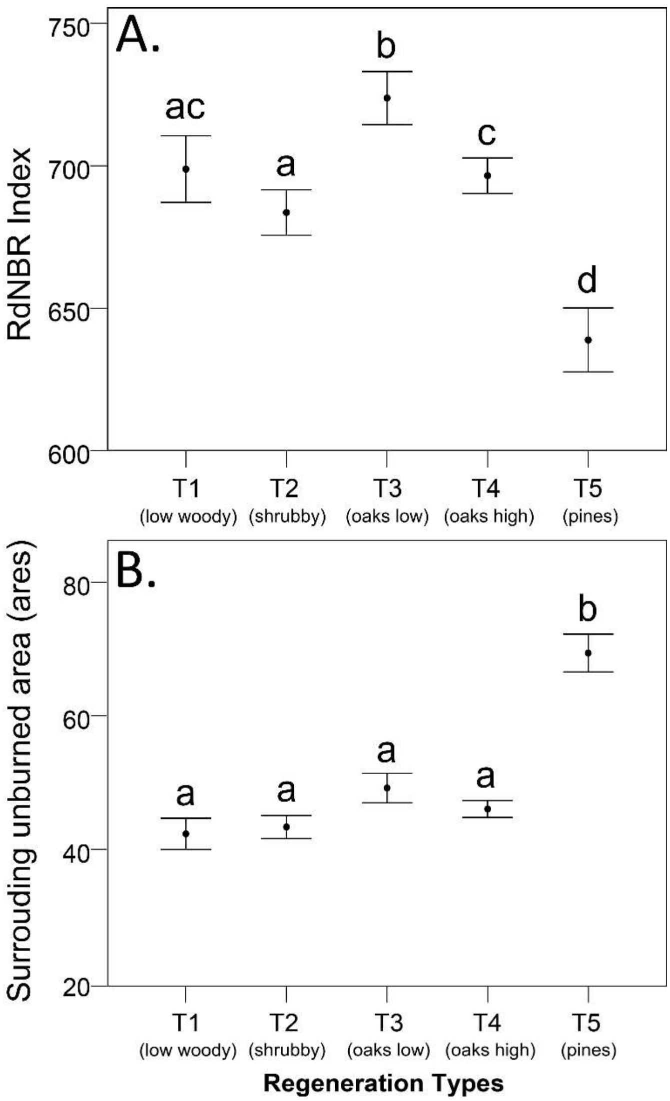

Fig. 5. Mean (± S.E.) values of the two covariates related to fire effects (A, burn severity as RdNBR index; B, surrounding unburned area) for the plots classified in each of the regeneration types. Different letters indicate significant differences among types according to the Kruskal–Wallis post-hoc tests for all pairwise comparisons.

3. 4. Relative importance of the different factors on the regeneration trajectories

Our models yielded overall accuracy rates ranging from 68.4% to 72.8% (i.e., OOB error estimate rates ranging from 27.2% to 31.6 %), with the occurrence of regeneration types presenting high cover of tree species (oaks in T4 and pines in T5) the most accurately predicted by the set of topographic, pre-fire vegetation, and fire-related factors (Table 4). The most important variable differentiating the sites with low woody vegetation cover from the rest was elevation (Table 4), which confirmed that this regeneration type is strongly bound to upper-slope sites, probably in mountain ridges or hilltops (which also meet the other important classification criteria, specifically low slopes, convexity and absence of marked aspects; Fig. 3A-D). These areas also showed a high percentage of non-wooded and cultivated areas in 1956 (Fig. 4A), and in general they burned at fairly high severity (Fig. 5A).

Table 4. Computed variable importance in the Random Forest model for predicting the occurrence of each regeneration type according to Model Improvement Ratio (MIR). Darker shading indicating higher variable importance. The overall out-of-bag (OOB) error estimates in each model are also reported.

Regeneration type	**T1 (low woody)**	**T2 (shrubby)**	**T3 (oaks low)**	**T4 (oaks high)**	**T5 (pines)**
Model OBB estimate of error rate (%)	30.6	30.7	31.6	28.6	27.2
Variable importance (MIR)					
(a) Topographic variables					
Elevation	1.00	0.93	0.66	1.00	0.63
Northness index	0.35	0.92	0.87	0.59	0.78
Slope	0.39	0.79	0.73	0.44	0.57
Terrain curvature index	0.23	0.36	-0.12	0.17	0.11
(b) Vegetation and land use					
1956 cover type	0.55	0.63	0.99	0.32	0.67
1995 Tree canopy cover	0.40	1.00	0.39	0.45	0.77
(c) Fire effect					
RdNBR index	0.51	0.18	1.00	0.41	0.99
Surrounding unburned area	0.15	0.93	0.30	0.29	1.00

In relation to the other post-fire vegetation types, areas dominated by shrubby vegetation (T2) were strongly driven by topographic variables and were predominantly found at mid-to-high elevations on south-facing slopes (Fig. 3A, Fig. 3C). They also occurred in areas where the pre-fire TCC was low (Fig. 4B) and in which the presence of neighboring unburned patches was scarce (Fig. 5B). Similarly to T1, land-use cover type in 1956 was an important driver for this type, which very often occurred in areas showing non-wooded and cultivated land (Fig. 4A). Topographic factors were also highly relevant variables differentiating T3 (low-to-moderate cover of oak regeneration) from the rest, with T3 areas locating to mid-to-upper-slope sites, mostly north-facing and/or with gentle slope (Fig 3A-C). Land-use cover type in 1956 (with high percentage of woodland) and burn severity (usually high) also appeared as decisive factors triggering the occurrence of T3 (Fig. 4A, Fig. 5A). The occurrence of a high cover of oak regeneration (T4) was mostly driven by elevation but, contrary to T1, this regeneration type was bound to lower-slope sites and valley bottoms, mostly on north-facing slopes (Fig. 3A-C). Other important but less determinant characteristics of the sites regenerated as T4 were that they burnt at lower severity than T3 (Fig. 5A) and presented higher pre-fire TCC than any other types (Fig. 4B). Finally, the occurrence of pine regeneration (T5) was fundamentally driven by attributes related to fire effects (Table 4). T5 appeared mostly in sites burned at lower severity and surrounded by substantial areas of unburned patches (Fig. 5B). Pre-fire vegetation factors were also very important for the occurrence of T5 which, similarly to T4, appeared in sites having a long history of tree cover and high pre-fire TCC (Fig. 4A-B). In terms of topographic factors, pine regeneration appeared preferentially in quite steep mid-to-upper-slope sites but not on pure north-facing or on marked south-facing sites (Fig. 3A-C).

4. Discussion

4. 1. Post-fire regeneration of black pine

Fifteen years after the wildfire, a relatively small proportion of the studied area showed black pine regeneration despite black pine having been the main tree species before the fire event. This corroborates the low ability of this non-serotinous pine species to efficiently respond to high-severity crown fires (Retana et al., 2002; Savage and Mast, 2005; Pausas et al., 2008). We nevertheless found some sites throughout the study area where abundant pine regeneration occurred, mostly corresponding to zones that burnt at lower severity than the rest and that were close to unburned patches. This result confirms the adaptability of this species to surface fires and the ability it presents to recruit from the seeds supplied by surviving individuals. The dependency of pine regeneration to the presence of unburned patches has already been reported in previous studies (Ordóñez et al., 2006; Vilà-Cabrera et al., 2011) and is explained by the relatively limited seed dispersal distance of this species. In the case of black pine, the surviving adult trees may also shield seedlings against direct sun exposure and thus favor their establishment and survival, according to their intermediate shade-tolerant character (Niinemets and Valladares, 2006) and low ability to colonize very open spaces (Ordoñez et al., 2004; Tiscar and Linares, 2014).

Our results show that patches presenting abundant pine regeneration also occurred in areas with low-to moderate presence of resprouting species and thus relatively free of competition from these resprouters in the early post-fire period (Gracia et al., 2002; Ordoñez and Retana, 2004). Prior to the fire, these areas may have corresponded to pure pine stands with a poorly developed understory layer, which would partly explain why they burnt at lower severity than others (Broncano and Retana, 2004; Lentile et al., 2006). On the other hand, the higher occurrence of abundant pine regeneration in sites with a long history of forested cover might be related to the higher probability of the presence of mature trees in the surrounding unburned patches (Stephens et al., 2009). Mature trees are known to produce large amounts of cones when they remain in highly exposed conditions, such as in small isolated patches surrounded by burnt area (Ordoñez et al., 2005). Finally, we found an important effect of topographic factors on pine regeneration, but this effect seemed to be highly variable depending on local climate and microsite conditions. For instance, we found the highest occurrence of pine regeneration on neutral exposures (W and E), whereas Gracia et al. (2002) reported that the post-fire regeneration of black pine occurred almost exclusively in wet north-facing slopes. In our study area, regeneration in north-facing slopes was mostly dominated by oak sprouts and fast-growing shrubs, which may have exerted severe competition on the pine seedlings during the first years after the fire.

4. 2. Vegetation shift and alternative regeneration trajectories

Post-fire regeneration trajectories dominated by woody vegetation types other than pine are prevalent in sites where pine was unable to regenerate. Grassland communities, in contrast, appear rarely and are usually restricted to very specific site conditions (mountain ridges or hilltops, rocky sites), mostly in areas that were not forested prior to the fire. In the expected scenario of an increasing occurrence of large crown fires in these systems, fire-mediated reversion of black pine stands into other types of woody vegetation (shrublands or forests dominated by resprouting tree species) is expected to happen more and more frequently, as already seen in other non-serotinous pine forests hit by crown fires in different temperate regions of the world (Trabaud and Campant, 1991; Strom and Fulé, 2007; Keane et al., 2008; Vacchiano et al., 2014). In our case, the vegetation shift from pine forest to shrubland is mostly mediated by the characteristics of the pre-fire vegetation and the topographic attributes of the burnt sites. This vegetation shift mainly occurred on young and relatively open pre-fire pine stands that have recently colonized old fields or open land and that, accordingly, were much less likely to undergone natural processes of species diversification by resprouting tree species prior to the fire (Puerta-Piñero et al., 2012; Navarro-González et al., 2013; Caldeira et al., 2014; Martín-Alcón et al., 2015b). These areas also burned at the lower end of the severity range, likely indicating lower fuel amount and lower abundance of hardwoods in the pre-fire stand composition (Broncano and Retana, 2004), and were far from unburned patches, thereby limiting the availability of pine seeds (Ordóñez et al., 2006). Finally, these sites mostly occurred in south-facing areas (in some cases with steep slopes) generally showing the poorest site quality (and lowest water availability), which may have hampered the establishment and growth of sprouting trees (Gracia et al., 2002; Gracia and Retana, 2004).

Around 60% of the burned area changed from pine to oak-dominated woods. This reflects the high availability of plant propagules of oaks and points to a fairly widespread presence of them (in the form of young recruits established under the pine canopy or adult individuals sharing the overstory with pines) in the pre-fire forest composition (Retana et al., 2002; Martín-Alcón et al., 2015b). Site quality (deduced by topographic attributes) was the most important component determining the cover of hardwoods regeneration in the post-fire community. However burn severity was also found to negatively affect hardwood cover probably due to increased mortality of the bud bank following high fire intensities (Espelta et al., 1999; Pausas and Keeley, 2014). The dominance of oak regeneration in the burnt area should nevertheless be interpreted with caution, since the typologies developed in Martín-Alcón et al. (2015a) differentiated regeneration types based on the relative cover of the dominant species/layer but did not consider the composition of the subcanopy or ground layers including the presence of small pines in regenerating areas dominated by shrubs or oak sprouts. Indeed, young pines are actually relatively frequent in these areas (personal observation). The recruitment of these pines probably began some years after the fire (especially in the most xeric sites) once the seedlings were able to benefit from a certain degree of protection from the oak canopy against direct exposure to sun (Gracia et al., 2002; del Cerro Barja et al., 2009; Tiscar and Linares, 2014; Martín-Alcón et al., 2015b). Mid- to long- term monitoring will be necessary to assess whether some of these areas evolve towards mixed pine-oak stands.

4. 3. Post-fire dynamics and management implications

This study provides an integrative landscape-level analysis of the main factors driving regeneration dynamics after crown fires in forests dominated by a non-serotinous pine species. The analysis underlines key roles of a number of variables that have been under-explored to date, specifically the role of land-use trajectories and pre-fire forest cover. Based on our results, important vegetation changes are to be expected in the near future in these type of pinewoods, particularly in areas such as the Mediterranean basin where the occurrence of catastrophic wildfires is predicted to further increase. These disturbances may lead to a mosaic of forest types (including shrublands, pinewoods, oak-dominated forests and pine-oak mixed forests) shaping a new forest landscape that may in some cases emerge as more heterogeneous and diverse than the pre-fire landscape (Turner et al., 1998;

Lloret et al., 2002). We found that the nature of these changes will strongly depend on the pre-fire characteristics (structure and composition) of the vegetation. This knowledge can be used to define preventive management strategies oriented to enhance the resilience of these forest stands. On the one hand, modifying the spatial distribution of fuel types across the landscape by creating more fragmented landscapes and generating strategic areas with less vulnerable stand structures may increase the abundance of unburned patches and modify their spatial distribution in the burned landscape (Ritchie et al., 2007; Strom and Fulé, 2007; Fulé et al., 2012), and thus favor pine regeneration. At the stand level, the natural establishment of late-successional tree species such as resprouting broadleaves could be favored by the implementation of silvicultural interventions designed to modify the overstory structure (Lookingbill and Zavala, 2000; Navarro-González et al., 2013; Martín-Alcón et al., 2015b). Finally, post-fire restoration measures to promote soil protection in low-quality sites may also help achieve a faster and more generalized recovery of the forest cover, as certain topographic factors such as slope or aspect also play an important role (presumably through their effects on soil moisture distribution) in driving the occurrence of shrublands or sites with low-density of tree regeneration.

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